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ECOLOGICAL DISTRIBUTION AND ALLOMETRIC GROWTH OF THE BLACK MUSSEL *SEPTIFER VIRGATUS* AT ASAMUSHI, NORTHERN JAPAN, IN RELATION TO WAVE EXPOSURE AND SHORE LEVEL[1]

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Ecological distribution, size structure and allometry were investigated for a population of the black mussel *Septifer virgatus* at 4 sites with different wave strengths on a rocky shore at Asamushi, Mutsu Bay, northern Japan. *Septifer virgatus* was found from the mid- to higher intertidal zone between -10 and $+70$ cm above the mean tide level. The vertical distribution range was wider and higher on the most exposed site (St. 1) than on the sheltered site (St. 4), showing a greater density and a thicker mussel bed on the former. The shell length of the same age class was greater at the exposed site, and decreased with the shore level. These population traits were consistent in 1992 and 1994. Allometric growth analyses for the mussels on the upper, middle and lower shore levels in the distribution zone at 2 sites, i.e., the most exposed and the sheltered sites, showed that the relative shell height and shell width to shell length were greatest at the lower level, and that both parameters were greater at the exposed site. The dry weight of the soft part in relation to shell length decreased with the shore level, whereas the dry weight of the shell was largest at the lower level at the both sites. The dry weights of the soft part and shell were greater at the exposed site than the sheltered site, when compared between mussels for comparative shore levels. The ratio of the dry weight of the soft part to shell weight increased with shell length, but mussels at the upper level of the zone had a lighter soft part for any given shell weight than those from the lower level at both sites. This paper discussed how environmental factors, mainly wave exposure and shore level, influenced the population characteristics by affecting the feeding period and changing physical stress such as exposure time, temperature and desiccation.

INTRODUCTION

On the exposed rocky intertidal shores in northern Japan, the mussel zones consist mostly of the black mussel *Septifer virgatus* (WIEGMANN) and a common blue mussel *Mytilus edulis** LINNAEUS. At Asamushi, it has been reported that *S.*

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* The common blue mussel in the central and northern parts of Japan has been regarded as *Mytilus edulis* by many authors. However, this species is sometimes referred to as *M. edulis galloprovincialis* or simply *M. galloprovincialis* (HOSOMI, 1977 ; KAJIHARA, 1994). In the present study, we tentatively treat the species as *M. edulis.*

virgatus occupies the upper part of the mussel zone, while *M. edulis* occupies the lower part (Hoshiai, 1961, 1964; Hoshiai *et al.*, 1965; Tsuchiya, 1979; Nishihira *et al.*, 1982). On moderately wave-exposed rocky shores in Wakayama Prefecture, central Japan, *S. virgatus* and a lower-intertidal mytilid, *Hormomya mutabilis* (Gould), form vertically contiguous mussel beds (Iwasaki, 1995a, b). On the mid-tidal level on exposed shores in Hong Kong, *S. virgatus* is reported to form a mussel zone (Liu and Morton, 1994; Morton, 1995).

Mytilus edulis is a world-wide temperate species, and forms prominent zones in the mid-intertidal to shallow subtidal zones, attaching firmly to hard rocks with byssal threads (Hoshiai, 1959, 1960, 1961, 1964, 1965; Seed, 1969; Suchanek, 1978, 1981, 1985; McDonald and Koehn, 1988; Seed and Suchanek, 1992; Lintas and Seed, 1994).

Local populations of *M. edulis* frequently differ in growth rates and sizes as well as in the morphology of the shells and weight of the soft part (Kautsky, 1982; Tedengren and Kautsky, 1986; Kautsky *et al.*, 1990). A large part of these variations seems to be caused by the effect of environmental factors such as temperature, salinity, food abundance and wave action (Harger, 1970; Seed, 1973, 1976; and Hosomi, 1977 for *M. galloprovincialis* Lamark). Towards progressively higher levels on the shore, growth of mussels was thought to be limited by reduced submergence, shorter feeding time and longer desiccation period during low tide (Kennedy, 1976; Griffiths, 1981; Franz, 1993).

Morton (1995) reported that on Hong Kong rocky shore *S. virgatus* ceased its growth in winter (January to March) and in summer (July) and suggested that growth rings are laid down on the shell surface. Lutz and Castagna (1980) and Brousseau (1984) demonstrated that the external growth ring in *Geukensia demissa* is produced annually. The shell growth has been studied using growth rings for various long-lived bivalves including *M. edulis* (Lutz, 1976; Lutz and Rhoads, 1980) and *Yoldia notabilis* (Nakaoka, 1992).

A considerable number of studies have been conducted on various aspects of Japanese *M. edulis* (e.g., Hoshiai, 1959, 1960, 1964; Hosomi, 1977; Tsuchiya, 1982, 1983; Hirano, 1983; Tsuchiya and Nishihira, 1985, 1986; Matsumasa and Nishihira, 1994; Takeda and Kurihara, 1994). Information about some aspects of population dynamics, mortality and reproductive cycle of *S. virgatus* are available only for a population in Hong Kong (Morton, 1995). Studies on recruitment and factors limiting the lower distribution limit of *S. virgatus* were conducted by Iwasaki (1994, 1995a, b) on the gentle rock slope on the Pacific coast of central Japan. However, the intensive studies of *S. virgatus* are still required to clarify its ecology, especially for the populations of Japanese waters with regards to ecological distribution, population dynamics and life history strategies.

The objective of the present study is to elucidate the population parameters of ecological distribution, size structure, density and allometric growth of the *S.*

virgatus population at different intensities of wave exposure and tidal level, for the purpose of providing basic information for ecological traits of this important but little studied species.

Materials and Methods

Field studies were conducted on the small rock islet of Hadakajima, near the Marine Biological Station of Tôhoku University at Asamushi in Mutsu Bay, northern Japan (40°53′ N: 140°50′ E). A westward wind is predominant throughout most of the year (Hoshiai, 1965; Nishihira *et al.* 1982). Therefore, the west shore of Hadakajima is generally wave-exposed and the east side is less exposed (Fig. 1). The shore of Hadakajima is divided into 4 categories according to scores of relative wave exposure calculated by Hoshiai (1965) based on the wind force and the frequency of wind direction. Four stations (Fig. 1 and also Fig. 2) with different

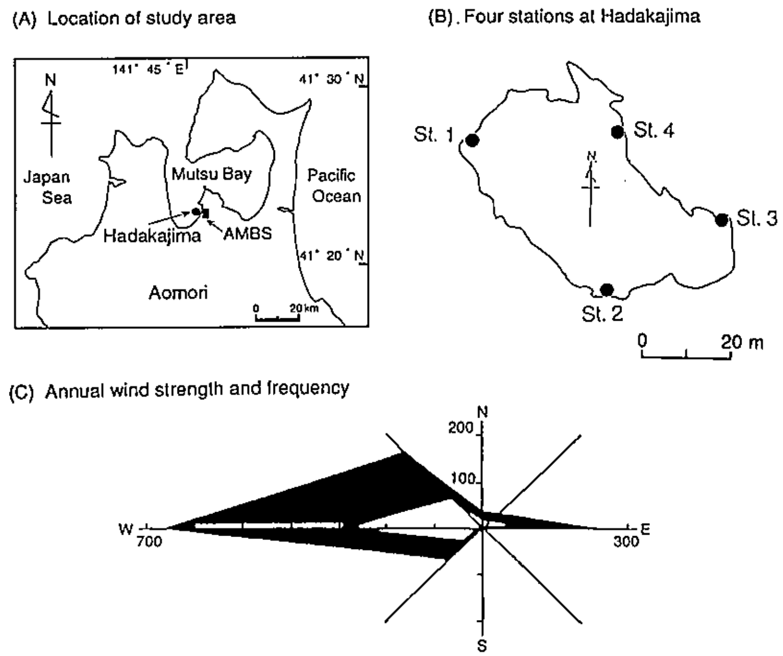

Fig. 1. (A): Location of the study area, Hadakajima at Asamushi, Mutsu Bay, Aomori, northern Japan. AMBS, Asamushi Marine Biological Station, Tôhoku University. (B): Four stations (Sts. 1 to 4) selected on the coast of Hadakajima where transect lines were set. (C): Annual total wind strength (black part) and frequency of the wind direction (white part) calculated by Hoshiai during 1959. The wind direction and wind intensity were observed twice a day, at 9:00 a.m. and 4:00 p.m. The wind intensity was classified into six classes by the appearance of the waves and breakers. The wind strength during 1959 was represented by the total of the mentioned class number showing the wind intensity in each of the eight directions.

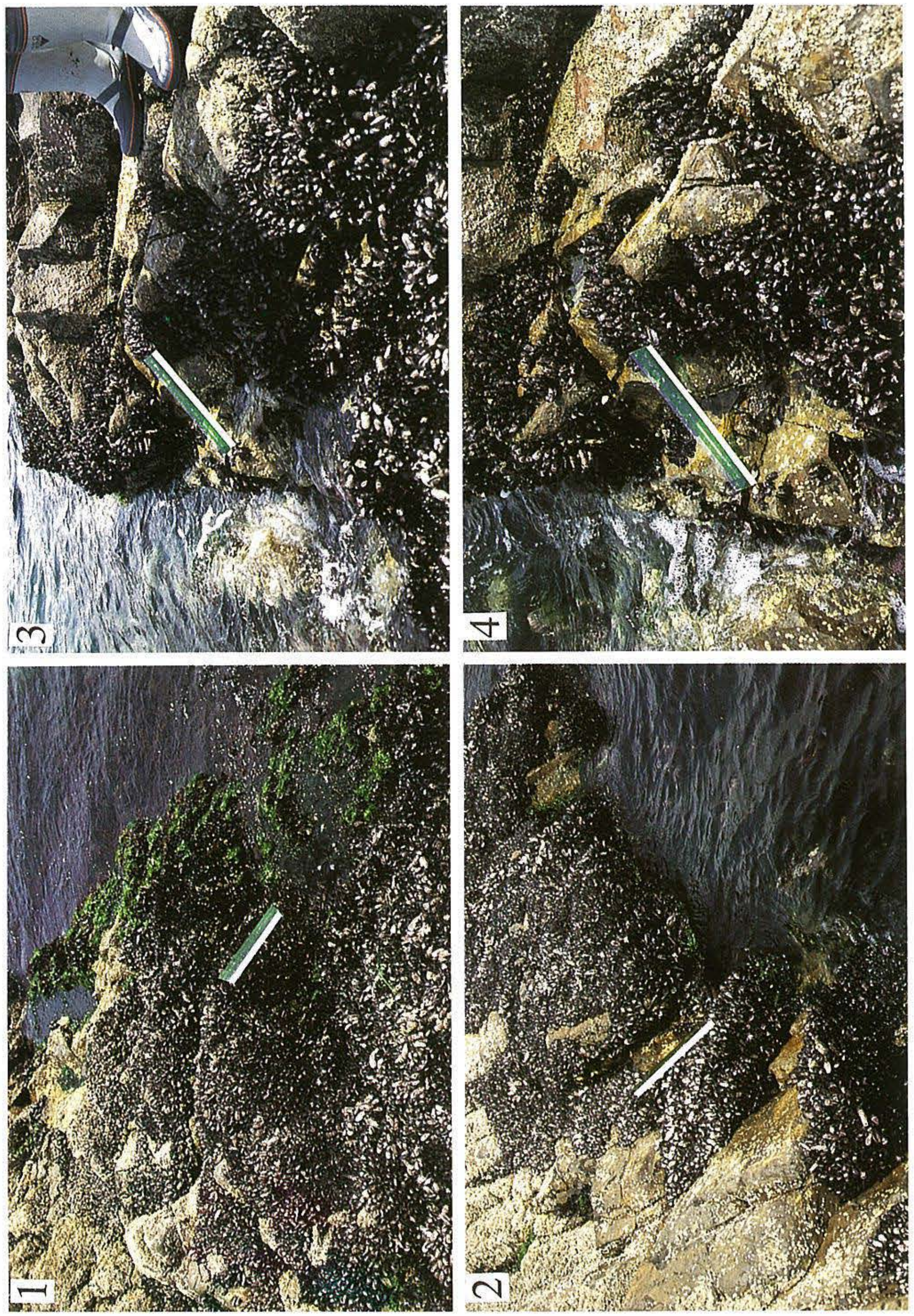

Fig. 2. Photographs showing the distribution of *S. virgatus* at each study station taken at low tide in May, 1995. Scale in the picture is 30 cm. 1, St. 1 (the most exposed site); 2, St. 2 (exposed site); 3, St. 3 (semi-exposed site); 4, St. 4 (the sheltered site) on Hadakajima.

intensities of wave exposure were selected.

Figure 1 shows the locations of the 4 stations on Hadakajima, together with the wind strength and frequency of wind direction (after Hoshiai, 1965) experienced during 1959. Station 1 selected on the west site is the most exposed site, Sts. 2 and 3 are moderately exposed and St. 4 set on the east shore is the least exposed or comparatively sheltered site among the 4 stations. Strictly speaking, there is not a sheltered shore at Hadakajima, in this study we treated St. 4 as the sheltered site for the sake of convenience. Figure 3 shows the estimated total submergence time at each tidal level of Mutsu Bay in 1994 calculated from the Tide Table (Japan Weather Association, Aomori Branch Office, 1993). The duration of submergence time decreases with tide level. The maximum tidal range was −49 to +49 cm above the mean tide level (MTL) in 1992, and −50 to +50 cm above the MTL in 1994. During the study period, it was observed that calm wave conditions were rare at the study sites, and that the exposed sites on Hadakajima were almost always washed over by small or large waves.

Field studies and sample collections were conducted during daytime low tides in June, 1992 and June, 1994. All of the sampling transects were selected on a typical *S. virgatus* bed at each station, and the 1994 sampling transects were set only 30 cm apart from the 1992 ones.

To quantify the density and vertical distribution patterns, samplings were performed at each station along a vertical transect set over the entire distribution range of the *S. virgatus* bed by continuously arranged 100 cm^2 quadrats. The

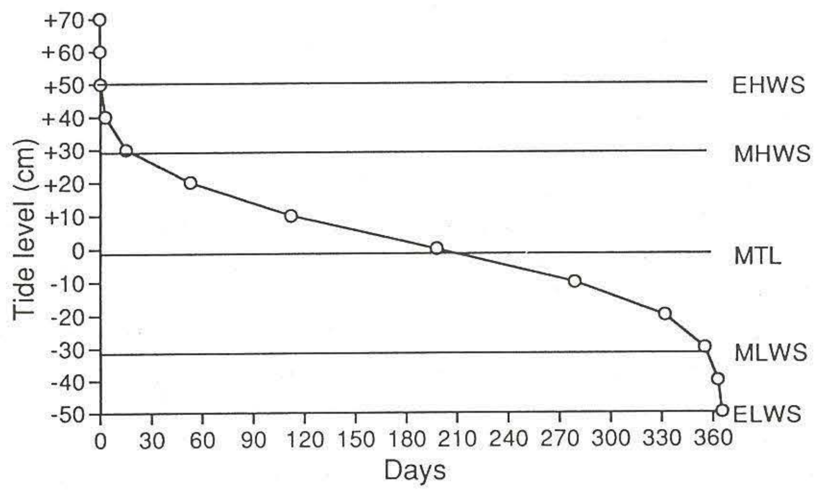

Fig. 3. Annual total submergence time (days) of the shore level of Hadakajima estimated according to the Tide Tables of 1994 for Aomori Bay (Japan Weather Association, Aomori Branch Office, 1993). EHWS, extreme high water level of spring tide; MHWS, mean high water level of spring tides; MTL, mean tide level; MLWS, mean low water level of spring tides; ELWS, extreme low water level of spring tide.

thickness of the mussel bed was determined by inserting a metallic rod vertically into the mussel bed until it reached the rock surface at 4 corners and the center of each quadrat. All mussels within the quadrat were scraped off by hands or using a spatula, placed in a plastic bag, and fixed in 10 % neutralized formalin. Firstly small individuals of the mussels were separated by washing the sample on a 1 mm mesh sieve under tap water. Then, the mussels remaining in the sieve were further separated into 2 parts by sieving with 5 mm mesh sieve. Byssal threads of the large mussels were also checked to separate the small individuals. Shell length was determined to the nearest 0.01 mm for all individuals using a digimatic caliper (Model CD-15C, Mitutoyo Corporation, Japan).

For allometric growth study, mussels were collected from 3 tidal levels of the vertical distribution zone of St. 1 (most exposed) and St. 4 (sheltered) in June 1994. At St. 1, mussels were collected from upper (+60 cm above the mean tide level), middle (+30 cm) and lower (-5 cm) tide levels. At St. 4, mussels were collected from upper (+30 cm), middle (+15 cm) and lower (+5 cm) tide levels. The levels in these 2 sites were not at the same tidal level, because vertical ranges of the mussel zones were different between 2 sites, since the vertical distribution of the mussels was wider at St. 1 (−10 to +70 cm above the mean tide level) than at St. 4 (−1 to +40 cm).

The following procedure was employed to measure the dry weight of the soft part (all tissues inside the shell excluding the byssus) and dry shell weight. For 3 shore levels, 50 mussels covering all size ranges were collected. Barnacles and other epizoites were removed from the shell surface and then rinsed with tap water. The shell length, shell height and shell width of each mussel (see Fig. 9A for definition) were measured with a digimatic caliper to the nearest 0.01 mm. The soft part was removed by dissection and placed onto pre-weighed paraffin paper. After removing the byssus, the soft part and shells were dried at 70°C for 48 h to a constant weight, and re-weighed using a Hansen Electronic Balance to the nearest 0.1 mg. The dry shells were then boiled for 20 min and the shell periosteum was removed to count the growth rings. The "major" growth rings on the external shell surface (see Fig. 7) were examined under a stereoscopic dissection binocular microscope (Nikon, model SMZ-2B, Japan) for the analysis of growth.

The density and bed thickness in relation to tide level were compared among stations and between the 2 sampling dates. The differences in the shell length in relation to the number of rings were examined among the 3 tidal levels at St. 1 and St. 4, and also compared for the same level of 2 stations. Test of homogeneity of variances among the treatments was tested by the F_{max} method. When the variances were not homogeneous, the Kruskal-Wallis test was used for the comparison of several samples and the Mann-Whitney U test was made for testing difference between 2 samples. For the allometric growth study, shell height, shell width, soft-part weight, shell weight, and ratio of soft-part weight to shell weight in relation to shell length were studied for the mussels from 3 levels at St. 1 and St. 4. The differences in the allometries among the 3 tidal levels and also between 2 stations were examined by ANCOVA. Post-hoc analysis was done to perform the Scheffe's S test.

Results

Vertical distribution

Figure 4 shows the shore profiles, vertical distribution ranges and densities of *S. virgatus* at the 4 stations. Station 1 is the most exposed among all the stations and had a gentle inclination. The vertical distribution range was from −5 to +70 cm above the MTL along the 1992 transect and from −10 to +63 cm along the 1994 transect (Fig. 4A). Station 2 is on the exposed site and its slope decreases gradually. Along the 1992 transect, *S. virgatus* was found between a tide level of 0 and +46 cm, and along the 1994 transect between −5 and +45 cm (Fig. 4B). Station 3 is semi-exposed with a relatively steep shore inclination (Fig. 4C). The mussel zone covered a range from 0 to +40 cm level along the 1992 transect, and from −2 to +38 cm along the 1994 transect. Station 4 is the sheltered site among the stations and

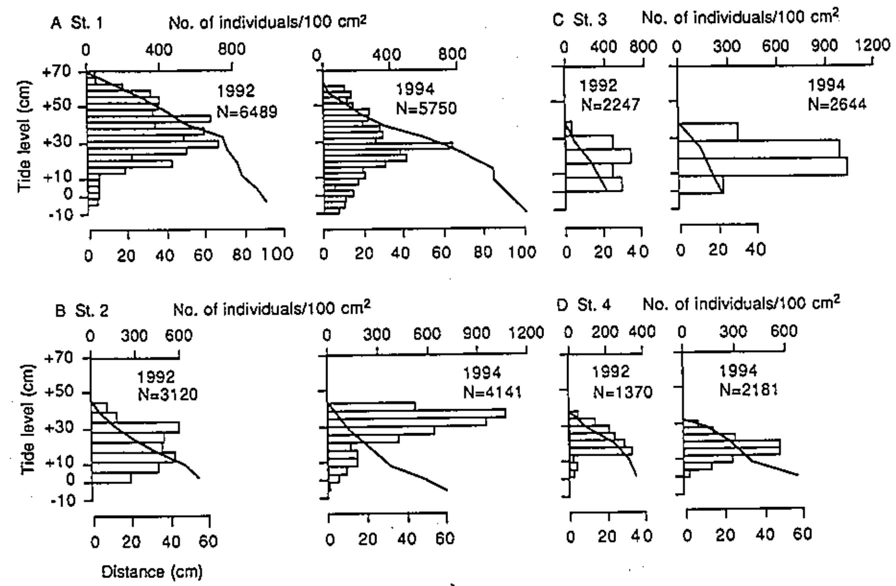

Fig. 4. Vertical distributions and densities of *S. virgatus* at the 4 stations on Hadakajima. Sampling was done by continuously set 100 cm² quadrats on June 3, 1992 and June 12, 1994. The 1994 transects were set 30 cm apart from the 1992 transects at each station. The bar graph shows the density at each tidal level, and the line graph the profiles along the transect lines. N = Total number of individuals. Each bar represents one quadrat (100 cm²).

its shore inclination is a little steep. Mussels were distributed between +2 and +40 cm along the 1992 transect, and between −1 and +33 cm along the 1994 transect (Fig. 4D).

The vertical distribution range was largest on the shore with stronger wave action (St. 1; −10 to +70 cm), while it was smallest at the sheltered site (St. 4; −1 to +40 cm).

At the lower part of the distribution zone of *S. virgatus*, very few small-sized (≦10 mm) *M. edulis* were found (1-3% of the total) living among *S. virgatus*.

Density

Table 1 shows that the distribution range of high density area (≧200 individuals/100 cm^2) was generally become larger with the wave exposure, having the greatest density at St. 1 and the smallest at St. 4. The tide levels of the maximum density was higher at Sts. 1 and 2 than at Sts. 3 and 4 (Table 1, Fig. 4A-D). Generally, the highest density was observed at the central part of each vertical distribution range, and the density decreased greatly toward the lower and upper parts of the distribution zone at all stations (Fig. 4A-D).

In 1992, a significant difference in density was found among the stations (Kruskal Wallis test, $p<0.04$), but no significant difference was found in 1994 ($p>0.05$). Along the 1992 transect, the highest density was found at the most exposed site (St. 1, Fig. 4A), while along the 1994 transect, it was observed at the exposed (St. 2) and semi-exposed (St. 3) sites (Table 1, Fig. 4B, C). In both years, however, density was lower at the sheltered site (St. 4) than in the exposed sites (Sts. 1-3) (Table 1, Fig. 4A-D). No significant difference in the density was found in 1992 and

Table 1. Distribution range (cm above mean tide level), high density (≧200/100 cm^2) range, maximum density, and tide level of the maximum density of *Septifer virgatus* along the transects at the 4 stations on Hadakajima.

Station	Transect (Year)	Distribution range (cm) (above mean tide level)	Range of high density (cm) (Tide level)	(Range)	Maximum density Number/100 cm^2	Tide level (cm)
1	1992	− 5 to +70	+15 to +62	47	719	+30
1	1994	−10 to +63	+ 8 to +50	42	769	+28
2	1992	0 to +46	0 to +32	32	595	+32
2	1994	− 5 to +45	+22 to +45	23	1,072	+38
3	1992	0 to +40	0 to +30	30	659	+20
3	1994	− 2 to +38	− 2 to +38	40	1,032	+15
4	1992	+ 2 to +40	+12 to +28	16	338	+15
4	1994	− 1 to +33	+10 to +25	15	568	+18

1994 when compared at the same station (Mann-Whitney U test, $p>0.05$).

Mussel bed thickness

The average thickness of the mussel bed in each quadrat is shown in Fig. 5. The mussels piled up on the top of other individuals and made a multi-layered mussel bed in the high density quadrats. Table 2 shows that the range of thick (≧5 cm) mussel beds was wider and the bed was thicker at the exposed sites (Sts. 1-3) than at the sheltered site (St. 4) (Fig. 5). At all stations, the thickest mussel bed

Table 2. Distribution range (cm above mean tide level) of thick (≧5 cm) mussel beds, maximum thickness and tide level of the thickest bed of *Septifer virgatus* along the transects at the 4 stations on Hadakajima.

Station	Transect (Year)	Range of thick bed (cm) Tide level	Range	Maximum thickness (cm)	Tide level (cm)
1	1992	+ 5 to +50	45	14	+35
1	1994	+ 8 to +45	37	10	+28
2	1992	+12 to +40	28	10	+30
2	1994	+15 to +45	30	14	+32
3	1992	+ 8 to +40	32	10	+20
3	1994	− 2 to +38	40	13	+22
4	1992	+10 to +25	15	7	+20
4	1994	+ 8 to +22	14	10	+15

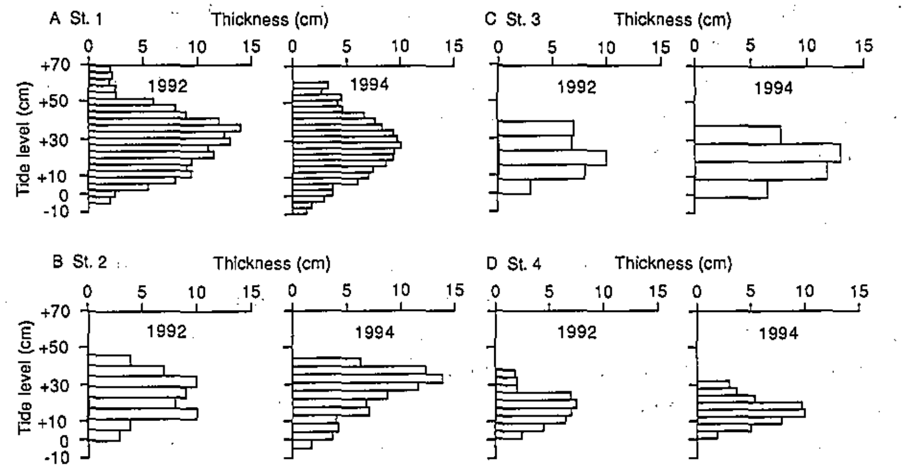

Fig. 5. Average thickness of the mussel beds of *S. virgatus* at the 4 stations on Hadakajima in 1992 and 1994. Each bar represents the average thickness for a quadrat (100 cm^2). Five measurements of the thickness were taken for each quadrat.

was found in the middle levels (Fig. 5). In the upper part of the mussel zone at each station, mussels were very compact, mostly forming a mono-layered bed. The mono-layered mussel bed was also found in the lower level of distribution zone at all stations. In 1992, a significant difference in the bed thickness was found among 4 stations (Kruskal-Wallis test, $p<0.01$), but no significant difference was found in 1994 ($p>0.05$). The bed thickness was not significantly different between 1992 and 1994 (Mann-Whitney U test, $p>0.05$). The mussel bed thickness was positively correlated with density of the mussels (see Figs. 4, 5).

Size structure

Figure 6 depicts the size compositions of *S. virgatus* in each quadrat at 4 stations for the 2 sampling years. The proportion of the small-sized mussels (≤ 12 mm in shell length) was greatest in both years. These mussels (≤ 12 mm) are thought to be one year old or less (see DISCUSSION). At the lower part of distribution zone, most of the large-sized mussels were >35 mm. Therefore, we arbitrarily divided the mussels into 3 size groups. Table 3 shows that the proportion of the small-sized mussels increased toward lower shore level at Sts. 1 and 4 in both years. When regression statistics of all stations (Sts. 1-4) were performed together, proportion of small individuals was greater at the lower shore in both years. In 1992, the proportion of the medium-sized (>12 mm and ≤ 35 mm) individuals was not significantly different with changes in tide level, except at St. 4 where it increased with the tide level. In 1994, the proportion of the medium-sized individuals was generally greater in the upper tide level at all stations except St. 2. When all stations were pooled, the medium-sized individuals increased with the tide level in 1994. The proportion of large-sized (>35 mm) individuals was not significantly different with changes in the tide level, but it was significantly greater at the lower level at St. 2 in 1994 and at St. 3 in 1992. A prominent peak in abundance of the individuals of 0-4 mm size class was seen in 1992 at all tide levels at all stations, while those of 6-10 mm size class were conspicuously abundant in 1994 at all tide levels and at all stations (Fig. 6A-D).

Growth ring

The relationships between mean shell length and number of major growth rings visible on the external shell surface (see Fig. 7) are shown for 3 shore levels (upper, middle and lower) of the mussel zone at Sts. 1 and 4 are shown in Fig. 8. The mussels were grouped into classes based on the number of major growth rings. For all classes, the shell length decreased with shore level at both stations (Fig. 8). At St. 1, for the same number of growth rings a significant difference was found in the shell length of the mussels of 3 tide levels except for the mussels with a single ring (Kruskal-Wallis test, $p<0.03$-0.001). At St. 4, the mussels also showed a significant difference among 3 tide levels except those with a single ring (Kruskal-Wallis test,

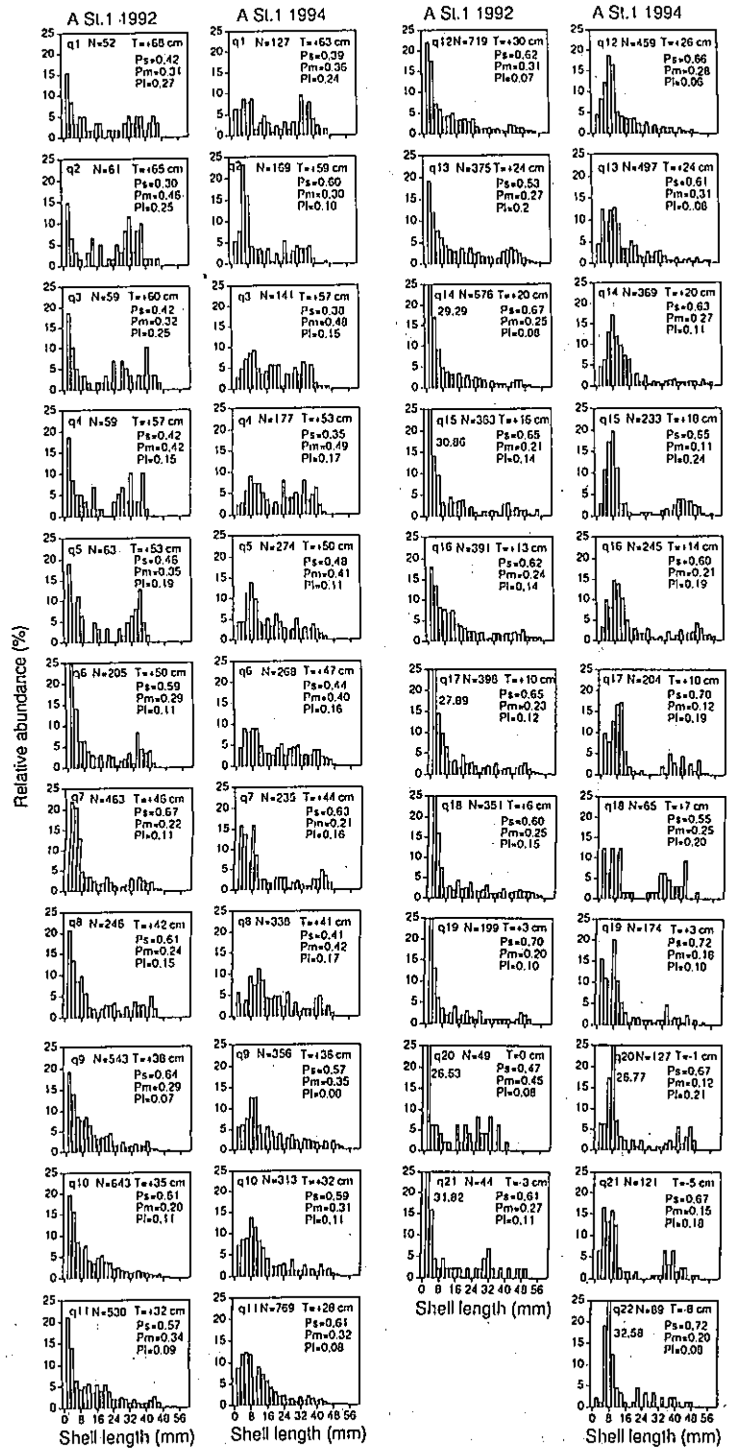

Fig. 6. See p. 116 for explanation.

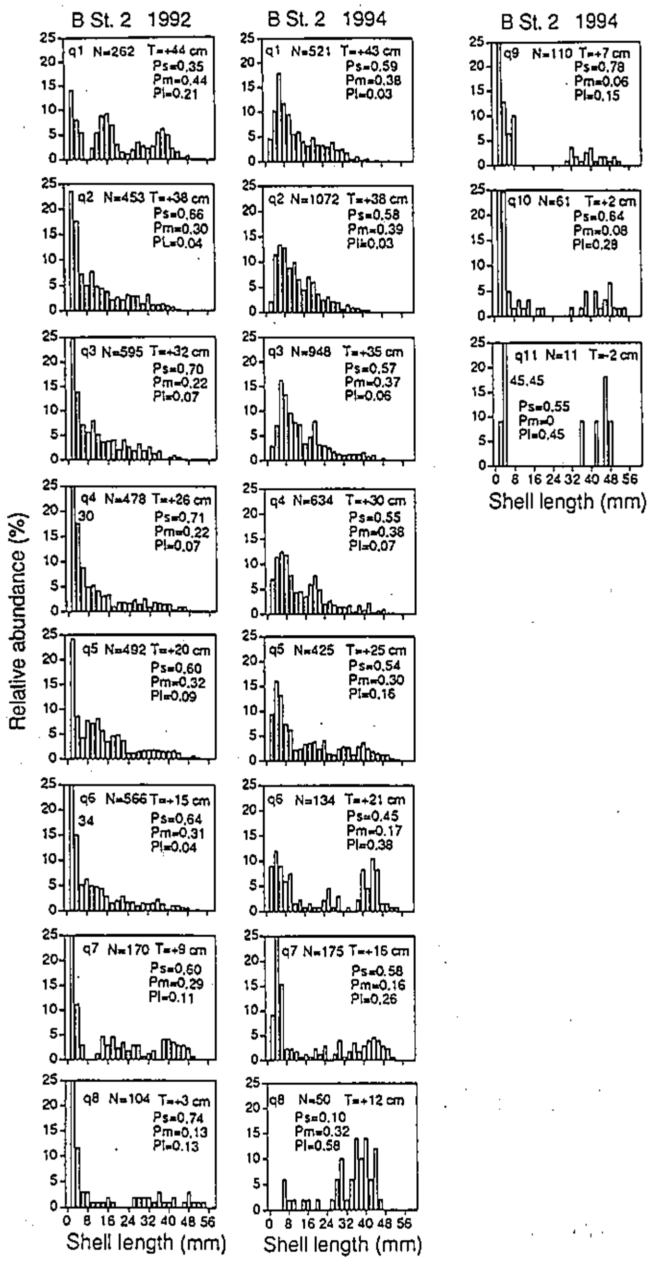

Fig. 6. Size frequency distribution of *S. virgatus* at the 4 stations on Hadakajima sampled on June 3, 1992 and June 12, 1994. The figure represents relative abundance of the mussels of each shell size class arranged from the upper to the lower shore. q, quadrat number from upper to lower tidal level; N, number of individuals/100 cm^2; T, tide level in cm above the mean tide level; Ps, proportion of small-sized ($\leq$12 mm shell length) individuals; Pm, proportion of medium-sized ($>$12 and $\leq$35 mm) individuals; Pl, proportion of large-sized ($>$35 mm) individuals.

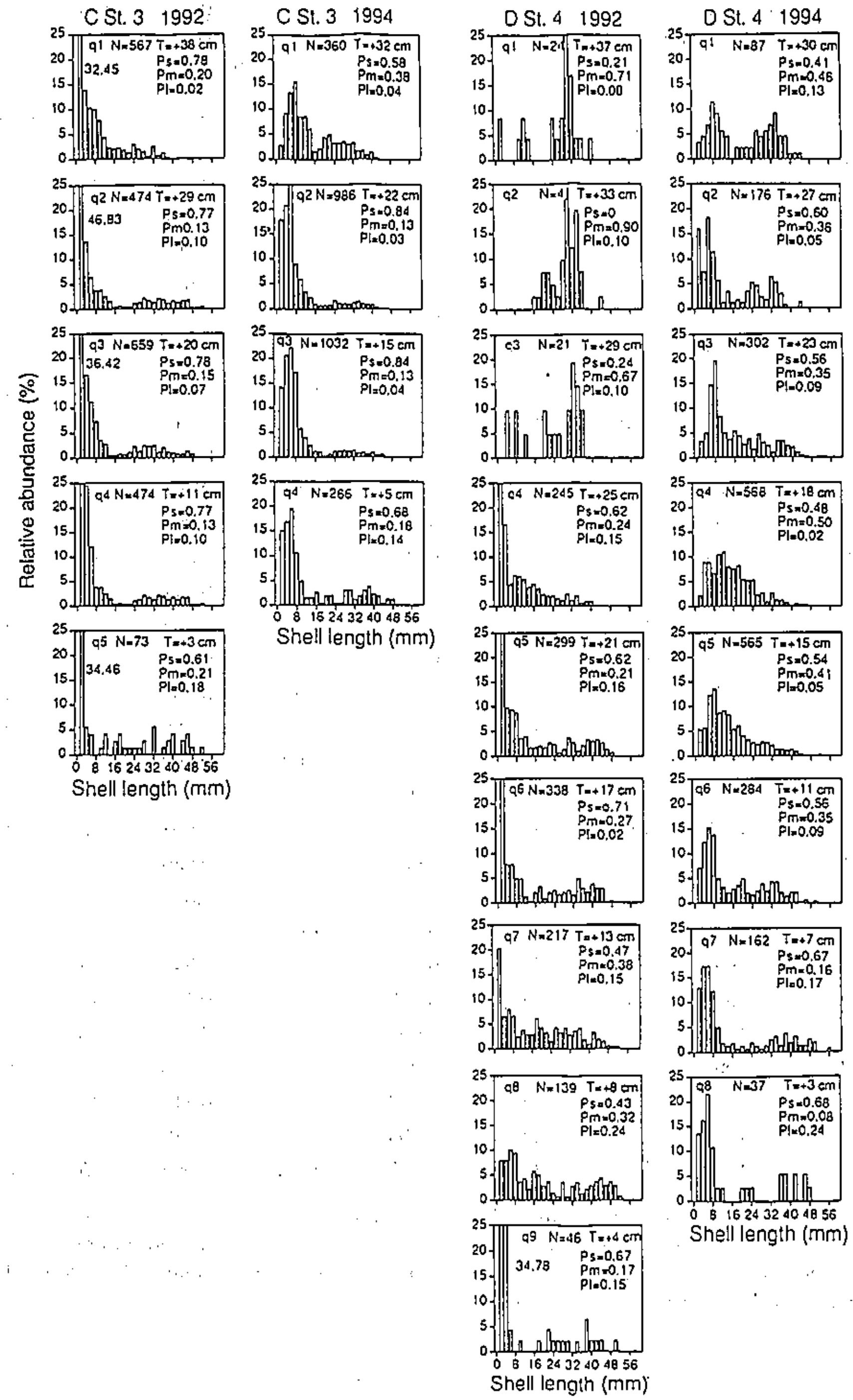

Fig. 6. See p. 116 for explanation.

Table 3. Regression statistics of the relationship between proportions of the individuals of three size groups (small, ≦12 mm shell length; medium, >12 mm to ≦35 mm; large, >35 mm) and tide level for *Septifer virgatus* on the coast of Hadakajima. Model of regression equation is Y=aX+b

Station	Year	Y	X	a	b	r^2	n	p
1	1992	Ps	Tl	−0.003	0.658	0.387	21	**
1	1992	Pm	Tl	0.001	0.151	0.171	21	ns
1	1992	Pl	Tl	0.002	0.091	0.360	21	ns
1	1994	Ps	Tl	−0.004	0.688	0.618	22	***
1	1994	Pm	Tl	0.004	0.167	0.636	22	***
1	1994	Pl	Tl	0.000	0.145	0.000	22	ns
2	1992	Ps	Tl	−0.003	0.693	0.137	8	ns
2	1992	Pm	Tl	0.004	0.190	0.344	8	ns
2	1992	Pl	Tl	−0.000	0.116	0.006	8	ns
2	1994	Ps	Tl	0.000	0.532	0.001	11	ns
2	1994	Pm	Tl	0.009	0.058	0.800	11	***
2	1994	Pl	Tl	−0.009	0.400	0.531	11	***
3	1992	Ps	Tl	0.004	0.666	0.541	5	ns
3	1992	Pm	Tl	−0.000	0.164	0.002	5	ns
3	1992	Pl	Tl	−0.004	0.168	0.750	5	*
3	1994	Ps	Tl	−0.004	0.802	0.104	4	ns
3	1994	Pm	Tl	0.007	0.076	0.426	4	ns
3	1994	Pl	Tl	0.003	0.122	0.569	4	ns
4	1992	Ps	Tl	−0.015	0.750	0.488	9	*
4	1992	Pm	Tl	0.018	0.066	0.594	9	*
4	1992	Pl	Tl	−0.003	0.182	0.230	9	ns
4	1994	Ps	Tl	−0.007	0.674	0.531	8	*
4	1994	Pm	Tl	0.011	0.144	0.573	8	*
4	1994	Pl	Tl	−0.005	0.181	0.348	8	ns
all	1992	Ps	Tl	−0.003	0.655	0.136	43	*
all	1992	Pm	Tl	0.002	0.240	0.086	43	ns
all	1992	Pl	Tl	0.001	0.103	0.072	43	ns
all	1994	Ps	Tl	−0.003	0.655	0.211	45	**
all	1994	Pm	Tl	0.005	0.157	0.489	45	**
all	1994	Pl	Tl	−0.002	0.187	0.065	45	ns

n, number of quadrats; p, significant level of regression coefficient (***, $p<.001$; **, $p<.005$; *, $p<.05$; ns, not significant); Ps, proportion of small individuals; Pm, proportion of medium individuals; Pl, proportion of large individuals; Tl, tide level (cm); all, four stations pooled together.

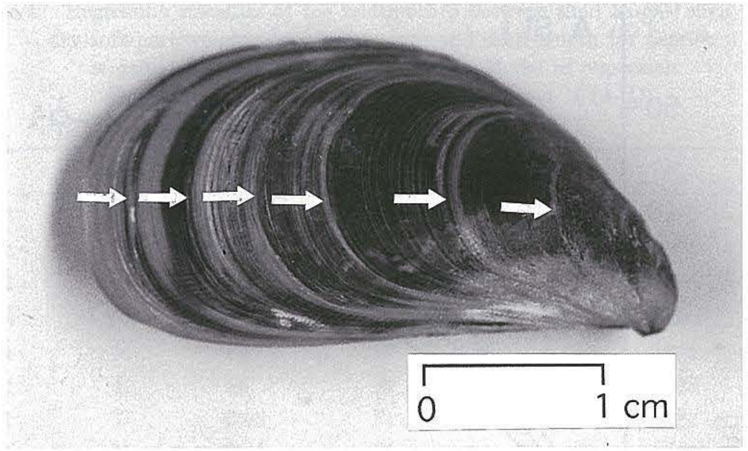

Fig. 7. The right shell valve of *S. virgatus* collected on November 15, 1994 from the middle level at St. 4. Arrows show major growth rings on the outer shell surface. The shell is 34.5 mm long and has 6 major growth rings.

$p<0.04$-0.001). The actual tidal levels of the upper and middle levels of the mussel zone at St. 1 (the most exposed site) were higher than those at St. 4 (sheltered). The actual tidal level of the middle shore level (+30 cm above the MTL) at St. 1 corresponded to the upper shore level (+30 cm) at St. 4. Even so, the shell length of the mussels of the same age class (those with same number of growth rings) was greater at all 3 levels at St. 1 than at St. 4 (Fig. 8A, B). For example, the average shell length of the mussels with 10 major rings at the upper, middle and lower levels were 39.09 ± 2.76, 47.83 ± 3.23 and 49.81 ± 2.70 mm, respectively at St. 1, whereas these were 37.24 ± 20.00, 43.01 ± 1.25 and 46.61 ± 2.29 mm, respectively at St. 4. At the upper and middle levels, shell length was not significantly different between Sts. 1 and 4 when compared for the same level (Mann-Whiteney U test, $p>0.05$). At the lower level, only the mussels with 5, 6, 7 and 9 rings showed significant difference between Sts. 1 and 4 (Mann-Whiteney U test, $p<0.05$-0.005).

Allometric growth

The shell height, shell width, dry weights of the soft part and the shell in relation to shell length were determined for the mussels at the upper, middle and lower levels of Sts. 1 and 4. The regression statistics of the graphs in Figs. 9, 10 and 11 are shown in Table 4.

Shell dimensions: Linear dimensions of shell height and shell width in relation to shell length are shown in Fig. 9. For the same shell length, shell height decreased with shore level. At Sts. 1 and 4, the shell height was significantly different among the 3 levels in the mussel zone (ANCOVA, $p<0.001$). At 3 tide levels, shell height was significantly greater at St. 1 than at St. 4 when compared for the same tide levels

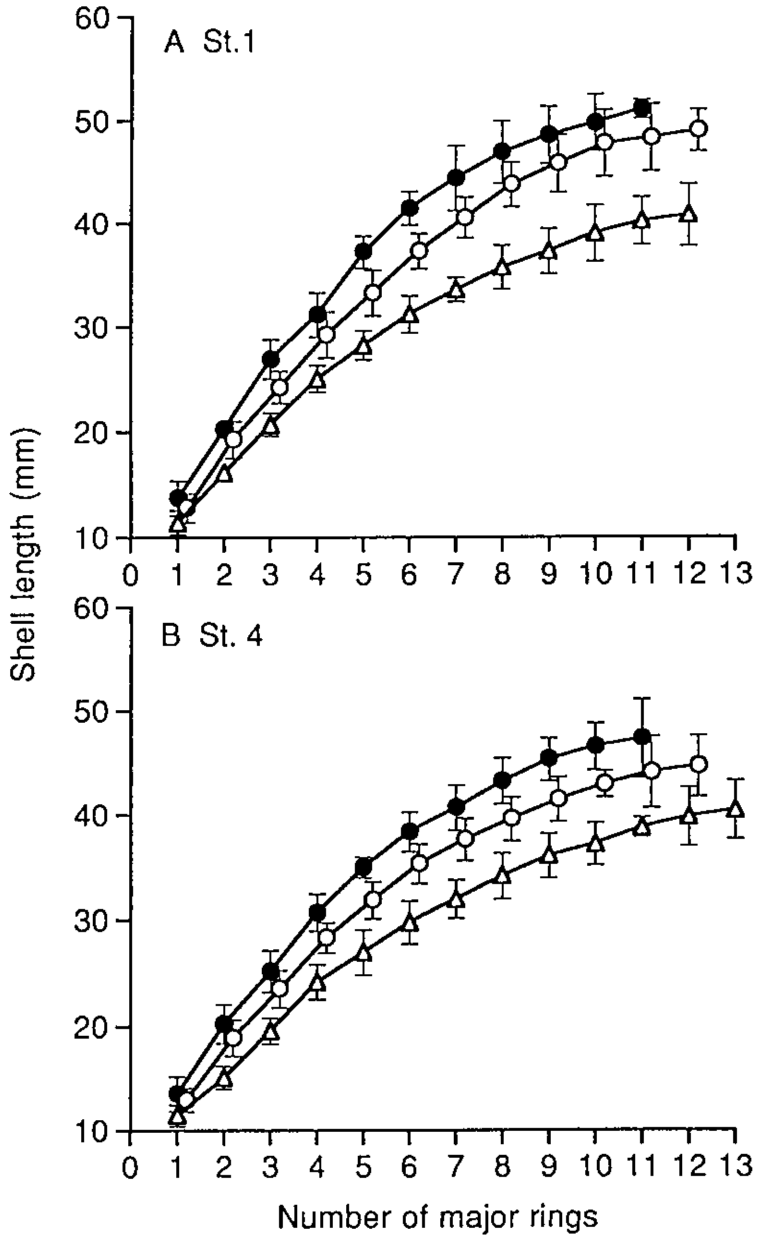

Fig. 8. Relationship between shell length (mean±SD) and number of major growth rings of *S. virgatus* at 3 shore levels of St. 1 (upper level, +60 cm; middle level, +30 cm; lower level, −5 cm) and St. 4 (upper, +30 cm; middle, +15 cm; lower, +5 cm) on Hadakajima in June 1994. △, Upper; ○, Middle; and ●, Lower level.

Table 4. Regression statistics of the relationship between shell height, shell width, dry soft part weight, dry shell weight and shell length for *Septifer virgatus* on the coast of Hadakajima. Model of regression equations are $Y=bX^a$ for Figs. 9 (A-D) and 10 (A-D), and $Y=aX+b$ for Fig. 11 (A-B).

Figure	Shore leve	Y	X	a	b	r^2	n	p
9A St. 1	U	Sh	Sl	0.735	1.047	0.975	50	***
9A St. 1	M	Sh	Sl	0.739	1.101	0.975	50	***
9A St. 1	L	Sh	Sl	0.721	1.295	0.983	50	***
9B St. 4	U	Sh	Sl	0.730	0.969	0.960	50	***
9B St. 4	M	Sh	Sl	0.739	1.013	0.982	50	***
9B St. 4	L	Sh	Sl	0.768	1.015	0.978	50	***
9C St. 1	U	Swd	Sl	0.962	0.465	0.984	50	***
9C St. 1	M	Swd	Sl	0.981	0.429	0.991	50	***
9C St. 1	L	Swd	Sl	0.959	0.508	0.983	50	***
9D St. 4	U	Swd	Sl	0.968	0.431	0.988	50	***
9D St. 4	M	Swd	Sl	0.950	0.425	0.976	50	***
9D St. 4	L	Swd	Sl	0.940	0.502	0.989	50	***
10A St. 1	U	Spwt	Sl	2.692	0.018	0.953	50	***
10A St. 1	M	Spwt	Sl	2.717	0.019	0.967	50	***
10A St. 1	L	Spwt	Sl	2.885	0.019	0.962	50	***
10B St. 4	U	Spwt	Sl	2.879	0.009	0.970	50	***
10B St. 4	M	Spwt	Sl	2.740	0.018	0.979	50	***
10B St. 4	L	Spwt	Sl	2.718	0.023	0.973	50	***
10C St. 1	U	Swt	Sl	2.674	0.191	0.982	50	***
10C St. 1	M	Swt	Sl	2.618	0.234	0.993	50	***
10C St. 1	L	Swt	Sl	2.576	0.305	0.990	50	***
10D St. 4	U	Swt	Sl	2.680	0.175	0.953	50	***
10D St. 4	M	Swt	Sl	2.602	0.242	0.986	50	***
10D St. 4	L	Swt	Sl	2.493	0.379	0.975	50	***
11A St. 1	U	Spwt/Swt	Sl	0.098	0.000	0.575	50	***
11A St. 1	M	Spwt/Swt	Sl	0.110	0.001	0.591	50	***
11A St. 1	L	Spwt/Swt	Sl	0.116	0.001	0.775	50	***
11B St. 4	U	Spwt/Swt	Sl	0.090	0.001	0.746	50	***
11B St. 4	M	Spwt/Swt	Sl	0.091	0.001	0.760	50	***
11B St. 4	L	Spwt/Swt	Sl	0.092	0.001	0.875	50	***

n, number of individuals; p, significant level of regression coefficient (***, $p<.001$); St. 1, exposed site; St. 4, sheltered site. U, upper level; M, middle level; L, lower level. Sh, Shell height (mm); Swd, Shell width (mm); Spwt, Soft-part weight (mg, dry weight); Swt, Shell weight (mg, dry weight); Sl, Shell length (mm).

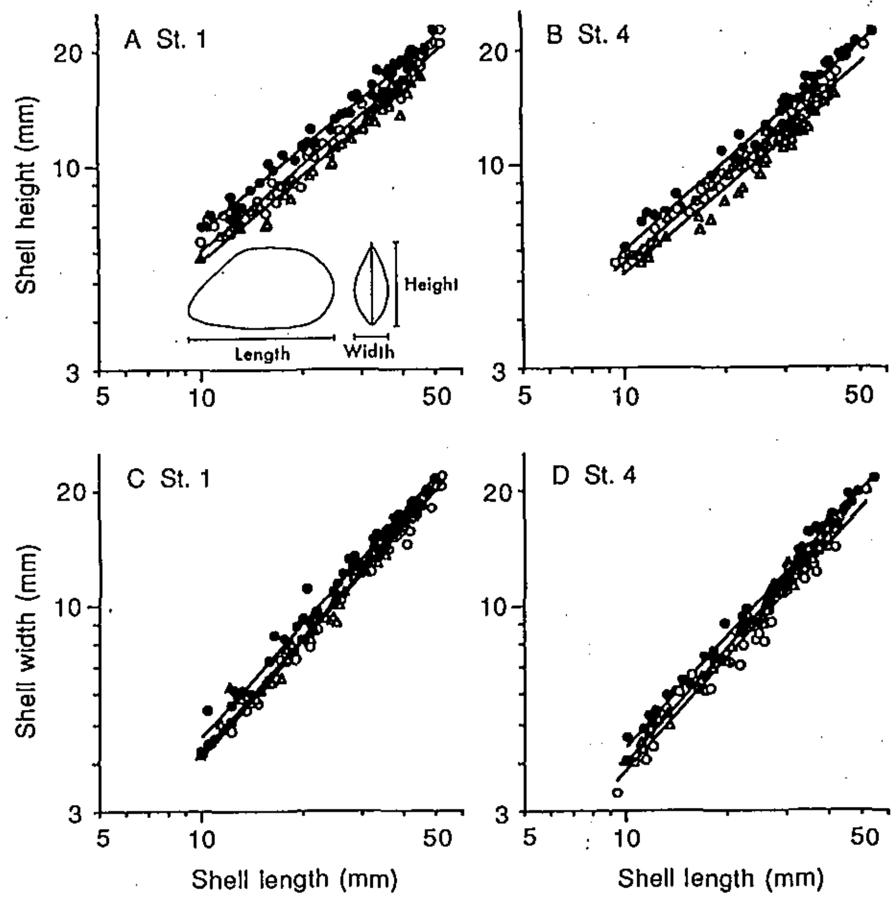

Fig. 9. Relationships between shell height (A and B) or shell width (C and D) and shell length of *S. virgatus* at 3 shore levels (△, Upper; ○, Middle; and ●, Lower level) of Sts. 1 and 4 on Hadakajima in June 1994.

(ANCOVA, $p<0.001$).

Shell width was greater at the lower level of the mussel zone at both stations (ANCOVA, $p<0.001$), but significant difference was not found between the upper level and the middle level (ANCOVA, $p>0.05$, Fig. 9C, D). Shell widths of the mussels at 3 tide levels were significantly greater at St. 1 than at St. 4 (ANCOVA, $p<0.001$).

Weight of soft part and shell: Figure 10 shows that the weights of the soft part and shell were positively correlated with shell length for all 3 levels of the mussel zones at both stations. The soft part and shell weights increased with shell length at all levels. At St. 1, the weight of the soft part of any shell length gradually decreased with shore level (ANCOVA, $p<0.001$) (Fig. 10A, B). At St. 4, the weight of the soft part of the mussels at the lower level was significantly greater than the

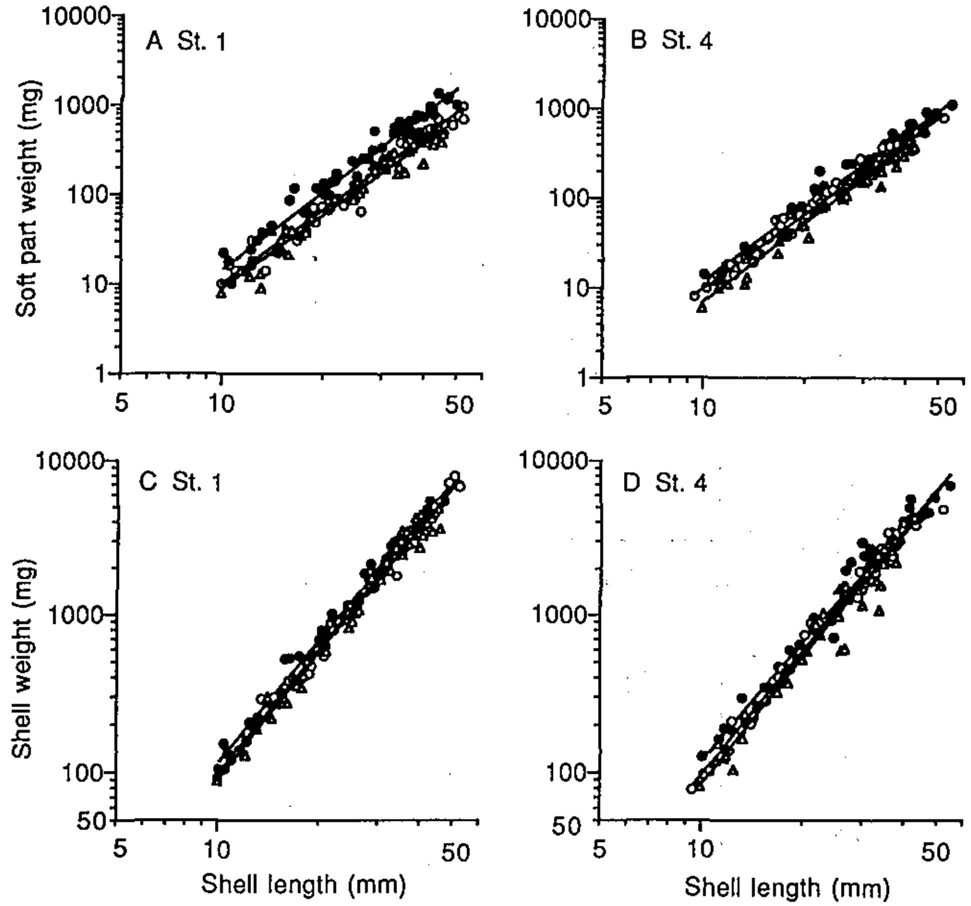

Fig. 10. Relationship between dry weight of soft part (A and B) or shell dry weight (C and D) and shell length of *S. virgatus* at 3 shore levels (△, Upper; ○, Middle; and ●, Lower level) of Sts. 1 and 4 on Hadakajima in June 1994.

weights at the upper and middle levels (ANCOVA, $p<0.001$), and the weights at the upper and middle levels were not significantly different (ANCOVA, $p>0.05$). At 3 levels, the weights of the soft part were significantly greater at St. 1 than at St. 4 (ANCOVA, $p<0.001$).

At Sts. 1 and 4, shell weights of the mussels at the lower level were significantly greater than those at the upper and middle levels (ANCOVA, $p<0.001$) (Fig. 10, Table 4), but no significant difference was found between the upper and middle levels (ANCOVA, $p>0.05$). Mussels at 3 levels of St. 1 had significantly greater shell weights than those of St. 4 (ANCOVA, $p<0.001$).

The larger mussels had greater ratio of soft-part weight to shell weight, but the ratio decreased with the shore level at both sites (Fig. 11, Table 4, ANCOVA, $p<0.001$). The ratio of the mussels from all 3 levels at St. 1 was significantly greater

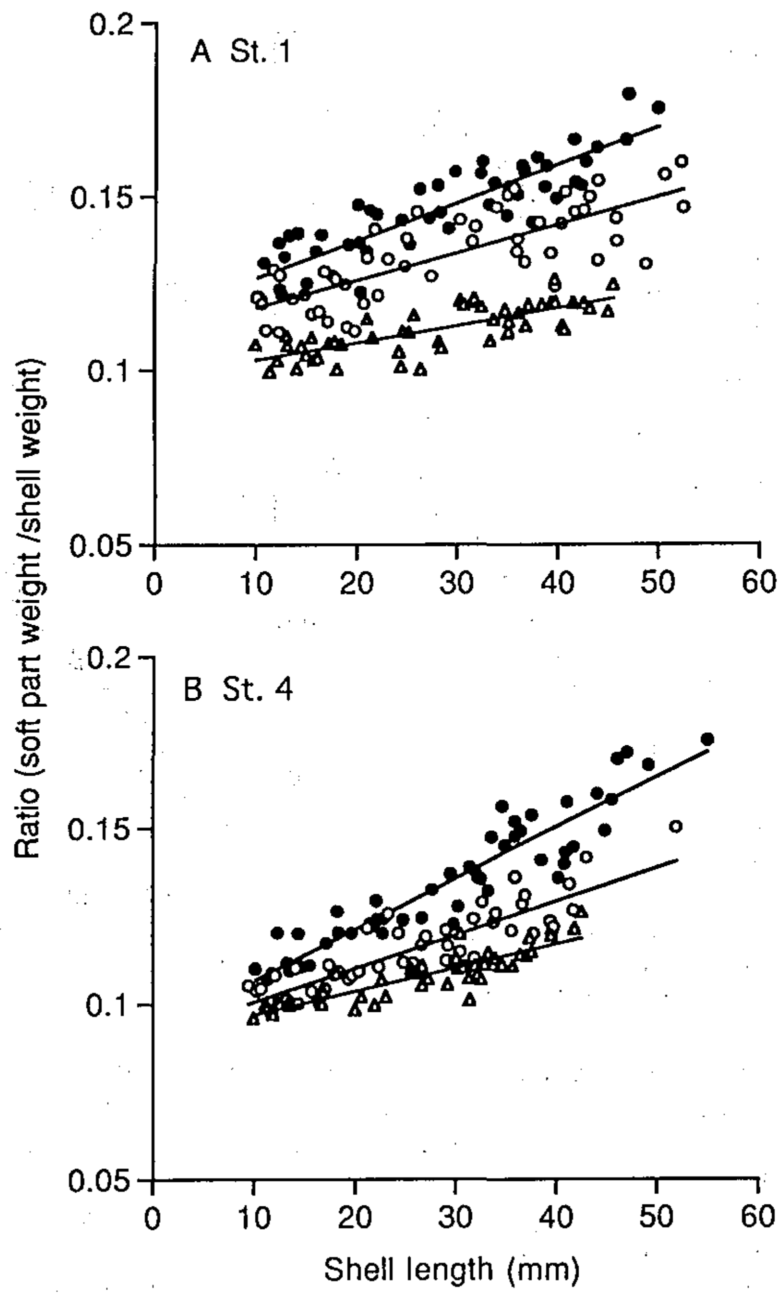

Fig. 11. Relationship between the ratios of soft part weight or shell weight to shell length of *S. virgatus* at 3 shore levels (△, Upper; ○, Middle; and ●, Lower level) of Sts. 1 and 4 on Hadakajima in June 1994.

than that at St. 4 (ANCOVA, $P<0.001$).

Discussion

Distribution, density and mussel bed thickness

The vertical distribution range of *S. virgatus* was different among the 4 stations on the shore around Hadakajima. It was largest at the most exposed site (St. 1), showing the highest upper limit but with a lower limit that was comparable to those at other stations. The vertical range was smallest at St. 4 (the sheltered site) (Fig. 4). Such a correlation between the vertical extent of the distribution range and the intensity of wave action has generally been accepted (see Lewis, 1964). Nybakken (1988) stated that strong wave action acts to extend the upper limits of the intertidal zone. Strong waves throw water further onto the shore than would normally occur as a result of high tide alone. The continual splashing at the exposed site allows the marine organisms to live at a higher position than in the sheltered site within an area with the same tidal range. This mechanism may explain the widening and upward shift of the upper limit of the vertical distribution range of *S. virgatus* with wave exposure. The density of the mussels was greater at Sts. 1-3 than at St. 4 in both years, suggesting a stable trend of the vertical distribution over the years.

It is generally accepted that the upper and lower distribution limits of intertidal organisms are governed by physical and biological factors, respectively (Connell, 1961a, b, 1972). It was reported that upper distribution of intertidal organisms might be limited by high temperature and desiccation (Connell, 1961a, b, 1972; Paine, 1974; Seed, 1969, 1976; Suchanek, 1978). In the mid-intertidal rocky shores in Hong Kong, a high mortality of *S. virgatus* occurred in summer (Liu and Morton, 1994; Morton, 1995). Higher mortality of *S. virgatus* was found at the upper part of mussel zone. The possible reasons would be the high temperature and desiccation (Liu and Morton, 1994; Morton, 1995). Mortality study of *S. virgatus* and *M. edulis* in the successive two years (1994 and 1995) at Hadakajima also showed that in summer the temperatures of mussel flesh were higher at the upper shore level resulting in higher mortality at higher level of the mussel zone (unpublished data). Accordingly, the physical factors such as high temperature, desiccation, longer exposure time to air may limit the upper distribution of *S. virgatus* at the higher shore.

Lower limit of intertidal animals has been thought to be delimited by competition with other species (Connell, 1961a, b, 1972; Hoshiai, 1961, 1964; Harger, 1968, 1970; Suchanek, 1978; Iwasaki, 1994, 1995a), and predation by starfish or muricid snails (Connell, 1961a, b, 1972; Paine, 1974, Seed, 1969, 1976). On the moderately wave-exposed gentle rock slope (5° inclination) in Wakayama Prefecture, *S. virgatus* inhabits the high to mid-intertidal level (Iwasaki, 1994, 1995a, b). In sheltered localities, there is a large amount of sediment accumulation, which might prevent the *S. virgatus* from settling (IWASAKI, 1994). In the present study area, accumulations of the sediment is not studied. However, since the rock had a steeper profile, this mechanism may not be true in the present study sites. An adverse effect of sedimentation on the recruitment seems unlikely on the coast of Hadakajima.

In the studies of mono- and mix-cultured *S. virgatus* and *M. edulis* in artificial cages (unpublished data), it was found that at the mid-intertidal (lower part of *Septifer* zone) and subtidal level the survivability and growth of *S. virgatus* were suppressed by *M. edulis*. Thus the lower limit of *S. virgatus* might be delimited also by the interspecific competition with *M. edulis* (unpublished data).

LUCKENS (1970) reported that the muricid gastropod, *Ocenebra japonica* (DUNKER) reached as high as the zone of the rock barnacle, *Chthamalus challengeri* HOEK, during at least a part of the year. Her experiment showed that *O. japonica* ate *M. edulis, S. virgatus* and various species of barnacles. TONG (1986) reported that on the rocky shores of Hong Kong, unquantified mortality of *S. virgatus* occurred from the predation of muricid gastropods (*Thais clavigera* and *Morula musiva*). These informations suggest that the lower delimit of *S. virgatus* at Hadakajima might also be partially limited by predators.

The effects of physical and biological factors seem comparatively less in the middle part of the mussel zone, and they in turn may make the mussel density greater there. Mussel bed thickness is related with density (see Figs. 4, 5), size structure and number of layers in the mussel clump. In the middle part, the mussel density (Fig. 4) and the number (not proportion) of large mussels were greater than in the upper and lower parts of the zone. The mono-layered mussel bed was found at the upper and lower parts, whereas the multi-layered bed was found in the middle part of the *Septifer* zone. Therefore, mussel bed thickness becomes thicker at the middle part of the mussel zone.

The distribution range and density of the mussels differed only slightly between the 2 sampling years. The observed slight differences seem to have been caused by the slight differences in microtopography of the near place where the transect lines were set (only 30 cm apart from each other).

Size structure

The density of *S. virgatus* was low in the lowermost part of distribution zone at all stations (Fig. 4). The proportion of the small-sized individuals ($\leqq 12$ mm) was greater at the lower level. Figure 8 shows that the shell length of the same-aged mussels was greater at the lower level and thus suggests that the individuals occupying the lower part of their distribution range grew faster than those in the upper parts of the range (Fig. 8). The faster growth at the lower level may give the greater proportion of larger individuals (>35 mm) at the lower shore level, and the higher proportion of medium-sized individuals at the higher shore levels (Fig. 6).

TSUCHIYA (1979) reported that at Hadakajima *M. edulis* became larger toward the lower tide level, and SENAWONG (1972) also obtained similar results for the mussel *Hormomya mutabilis* at Tanabe Bay, Wakayama Prefecture. But they did not discuss about mussel size in relation to their ages.

In 1992, the small mussels of $\leqq 4$ mm were dominant, while in 1994 those of 6 to 10 mm were dominant (Fig. 6A-D). The observed annual variation of the recruits might be caused by change in the major spawning period or larval and juvenile growth which may be affected by environmental factors such as water temperature. Actually, available oceanographic data showed that monthly average water temperatures from September 1991 to June 1992 were lower (4.1-21°C) than those from September 1993 to June 1994 (5.8-21°C) (data from Aomori Prefectural Aquaculture Research Center). Data were not available for the yearly change in food abundance and the effect of food availability on the growth of mussel larvae or juveniles, but the possible variation of food availability related to ambient temperature regime might affect the size of the small mussels. Therefore, studies on seasonal variations of spawning, settlement and juvenile growth related to ecological, physical and biological factors for some successive years are needed.

Growth

MORTON (1995) stated that on Hong Kong rocky shores the growth of *S. virgatus* occurred in 2 phases. Spring growth occurred from March to June in 1990 and from April to June in 1991. The growth ceased in the summers of both years and he suggested that this is presumably the time when a growth ring is laid down. Growth occurred again in late summer, i.e., from September to December 1989 and October 1990 to January 1991. Growth ceased over the winter months, i.e., from December 1989 to March 1990 and from January 1991 to April 1991, when the second shell growth ring is presumably laid down. LUTZ and CASTAGNA (1980) and BROUSSEAU (1984) demonstrated that the external growth ring in *Geukensia demissa* is produced annually. In Jamaica Bay, *G. demissa* ceases shell growth from November to April, and an externally visible growth ring occurs when new growth begins in May (FRANZ and TANACREDI, 1993).

On the rocky shore of Hadakajima, monthly shell growth increment of *S. virgatus* was measured from August 1994 to August 1995 (unpublished data). It was found that in various-sized mussels, the shell growth increment almost ceased during winter (from January to April) when water temperature became about 5-10°C, and the highest growth was found in summer (July to September) when water temperature rose up to about 20-24°C. At Asamushi, the temperate region, the growth of *S. virgatus* ceased only once a year in winter, from January to April, and started again from May leaving a visible ring on the shell surface. This indicates that the major rings were formed annually as in the case of other bivalves (LUTZ and CASTAGNA, 1980; BROUSSEAU, 1984; NAKAOKA, 1992; FRANZ and TANACREDI, 1993). Therefore, it is possible to age any individual of *S. virgatus* based on the number of major growth rings.

Based on the growth-ring analysis, it was found that the shell length of mussels in the same year class decreased with shore level at 2 stations (Sts. 1 and 4) with different wave exposures (Fig. 8). This is consistent with the findings of FRANZ (1993), who suggested that due to a longer submergence period the shell length of the same age class of *G. demissa* decreased with shore level. It was observed that in the mussel bed of Hadakajima, *S. virgatus* showed a faster growth toward the lower level of the zone (unpublished data). At the lower level, a lower density of mussels (Fig. 4A-D) and a longer submergence period (Fig. 3) might provide mussels with greater chance to acquire larger amounts of food, which might in turn facilitate faster growth.

Even though the upper and middle levels selected within the mussel zone of St. 1 (most exposed) were higher than those of St. 4 (sheltered), shells of the mussels in the same age class were larger at all 3 levels at the former station. It suggests that the shell growth increment of *S. virgatus* was greater at all 3 levels at the most exposed site than at the sheltered, when compared at the same levels of the distribution zone. It is supposed to be related to greater phytoplankton abundance and greater amount of total organic particulate at the most exposed site (unpublished data). In Osaka Bay, HOSOMI (1977) found that *Mytilus galloprovincialis* grew vigorously on wave-exposed surfaces, while on protected surfaces they were not so flourishing. He suggested that this observed difference might be caused by variations in the quantities of available nutrients. BOCK and MILLER (1995) reported that the changes in the quantity and quality of suspended materials associated with large waves are important for suspension feeders. When there are large waves, the shore is washed for a period, and large amounts of various types of food become available to the mussel. Thus, it is suggested that wave-exposure may make an exposed site a suitable habitat for *S. virgatus* along the coast of Hadahajima, because food availability and feeding period are greater and desiccation is less at the most exposed site than at the sheltered site when compared for the same shore levels (unpublished data).

Allometric growth

When compared among the mussels of same tidal levels, shell height and width in relation to shell length were larger at St. 1 than at St. 4. The influence of wave action is considered to be an important factor in determining shell shape and shell dimensions (FRANZ, 1993).

At Hadakajima, the relative shell height became smaller with shore level (Fig. 9A, B). The relative shell width was greatest at the lower level of the zone, but only slightly larger at the upper level than at the middle. In *M. edulis diegensis*, isolated (low density) individuals had greater shell height and width than those grown in the crowded conditions, where they were more slender (COE, 1946). Because of the low density at the lower level in the distribution zone, there is a sufficient space around the shell, and comparatively suitable habitat for food and smaller physical (desiccation and heat) stress may result in the greater shell height and width at the lower level. At the upper shore level, mussel density was low but shorter feeding time and greater physical stress might be responsible for the smaller shell height and width than at the lower level.

The weights of the soft part and shell in relation to shell length were greater at St. 1 than at St. 4 except at the lower shore (Fig. 10A-B). The weight of the soft part of the same-sized individuals gradually decreased with the shore level (Fig. 10A-B). Similar results, in the case of meat weight, were reported for *Mytilus edulis* (SEED, 1973, 1976), the ribbed mussel, *G. demissa* (FRANZ, 1993; FRANZ and TANACREDI, 1993), and the green-lipped mussel, *Perna canaliculus* (HICKMAN, 1979). It was suggested that the smaller growth rate of these bivalves at the higher shore level was due to exposure to hard physical and biological factors such as longer emergence period (HICKMAN, 1979; FRANZ, 1993), desiccation (SEED, 1973, 1976) and less availability of food (FRANZ, 1993; FRANZ and TANACREDI, 1993). These explanations seem to be applicable also to *S. virgatus* on the shore of Hadakajima.

The shell weight of *S. virgatus* in relation to shell length gradually decreased with the shore level. RAO (1953) suggested that calcium deposition is proportional to the duration of submergence, and may be independent of metabolic conditions, and consequently the shell weight should increase downshores. However, contradictory results were reported by BAIRD and DRINNAN (1957) and SEED (1973); the higher-shore *M. edulis* had heavier shells than the lower-shore mussels of equal shell length. They reported that similar-sized mussels from the upper shore were older, and older mussels had proportionately heavier shells. At Hadakajima, the same-sized mussel at the lower shore level had greater shell height and shell width than at the middle and upper levels (Fig. 9). Shell volume of *S. virgatus* of the same shell length was greatest at the lower shore level of Hadakajima (unpublished data). If a longer submergence time at the lower shore gives possibility of greater calcium deposition (RAO, 1953), the combined effect of shell volume and calcium deposition may explain the heavier shell of *S. virgatus* at the lower shore level of Hadakajima.

The ratio of soft-part weight to shell weight was smaller at the upper level of the mussel zone. BAIRD and DRINNAN (1957) and SEED (1973) showed similar results for *M. edulis*, and FRANZ (1993) for *G. demissa*. When emerged, the higher-shore mussels use their adductor muscle to close their shells for a longer time for protection against desiccation. Therefore, a loss of energy reduces the weight of the soft part more in higher-shore individuals than in the lower-shore ones (BAIRD and DRINNAN, 1957; SEED, 1973; FRANZ, 1993). Such adaptive behavior to the conditions of emergence may reduce the weight of soft part of *S. virgatus* at the upper shore level of Hadakajima.

At Asamushi, *S. virgatus* inhabits the highly exposed to moderately exposed rocky shores at the mid- and upper intertidal zones, but has not been found in completely sheltered shores such as inside the embankment of piers. The observed mussel distribution range, density, size structure, allomerty of shell and body weights were all different among the stations with different wave exposures and the 3 tidal levels in the distribution zone. More information on the general ecology including habitat preference, physiological tolerance, and biological factors (e.g., food availability, competition and predation etc.) are needed to elucidate the population traits of this little studied mussel. To investigate the mussel populations of Hadakajima, monitoring the natural populations and field experiments for the monthly recruitment, gonad maturation cycle, effect of environmental factors on seasonal growth in the mussels at 3 shore levels of exposed and sheltered sites are required. Moreover, to understand the causes for delimitation of the lower limit of the *S. virgatus* zone, investigation on interspecific competition of *S. virgatus* and *M. edulis* seems promising.

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